J. New York Entomol. Soc. 103(2):129–137, 1995

AGELAIA VICINA, A SWARM-FOUNDING POLISTINE WITH THE LARGEST COLONY SIZE AMONG WASPS AND BEES (HYMENOPTERA: VESPIDAE)

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Abstract.—Since von Ihering (1903, 1904), *Agelaia vicina* is famous for its huge nests, but no detailed account has been published. Several nests examined by us were mainly built in shelters but some were half to completely exposed. Main nest characteristics: envelope absent; combs large and horizontal with cells directed downwards; new combs mainly started synchronously and concentrically around several discoidal primordia (Fig. 2A, B, C, D, G); mature nests huge, eventually with more than 7.5 million cells; correspondingly colonies very populous, in Nest 3 described below 482,668 adults actually collected and the whole population estimated at over a million. The nest size (in cell number) and colony size (in adult number) of *A. vicina* is evidently unrivalled among all wasps and bees.

Key words: Agelaia vicina, Social wasps, Largest nest and colony sizes.

The genus *Agelaia* Lepeletier (= *Stelopolybia* Ducke, 1910 auct.; cf. Carpenter and Day, 1988) is the second largest genus (Richards, 1978) among Epiponini, neotropical wasps which found their nests by swarming. Its bionomics have been markedly clarified by Richards and Richards (1951), Richards (1971), Evans and West-Eberhard (1970), Jeanne (1970, 1973, 1975) and Jeanne and Fagen (1974) (reviewed by Jeanne, 1991). Concerning *A. vicina,* since a nest with 108,000 wasps studied by von Ihering (1903), virtually no information has appeared (see also Wenzel, 1992), doubtless because of its colossal size, reputed fierce disposition and dangerous massive attacks. Since 1972, we have examined some nests of *A. vicina.* Most were, when studied, already partly destroyed by local people. Nevertheless, as described below, some interesting data were obtained which may enrich our knowledge on the bionomics of this singular taxon.

RESULTS

A. Characteristics common to the nests

Most items below confirm the description by von Ihering (1903, 1904). 1—Nests generally built within shelters (Fig. 2A, F), but some in partly (Fig. 2D, E, G) or completely exposed (Fig. 1A, B, C) sites. 2—Envelope absent (but, see below). 3—

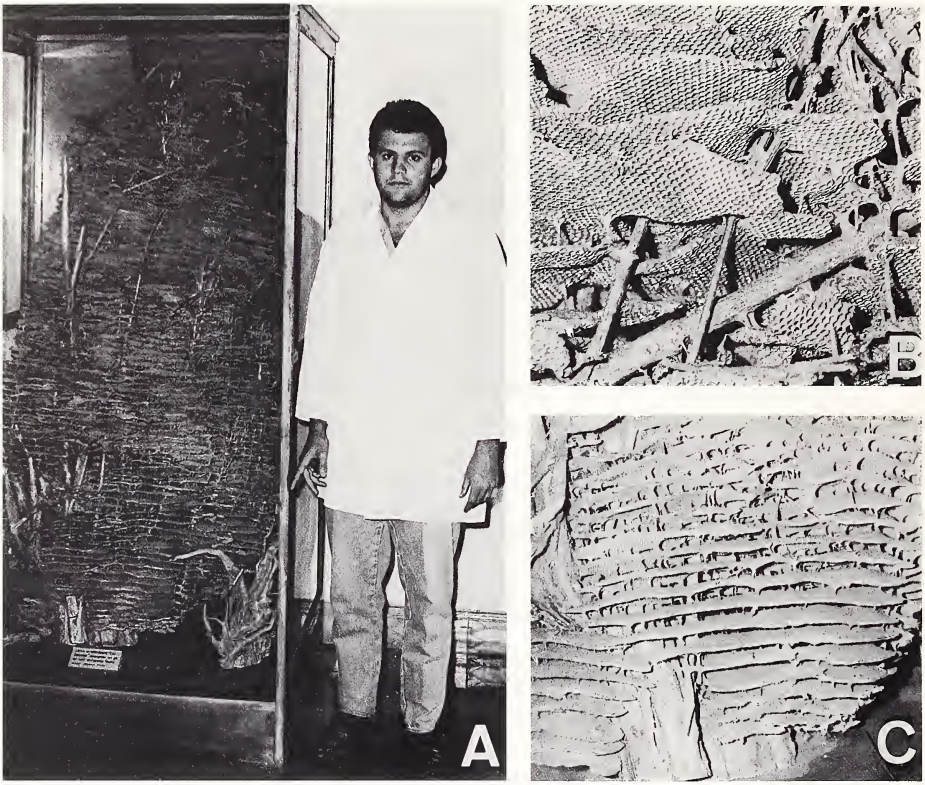

Fig. 1. *Agelaia vicina,* details of Nest 1: A, completely exposed nest involving a dead coffee tree; B, comb architecture around branches and twigs and C, nest's basal part showing horizontal combs, pillars, etc.

Although irregularly undulated and partly distorted, combs predominantly horizontal and fairly even (Figs. 1A, B, 2A–H) never convex and/or concave as in some congeners (Evans and West-Eberhard, 1970; Jeanne, 1973; reviewed by Wenzel, 1991). 4—Each comb predominantly started by synchronously building discoidal primordia, each hanging from the upper comb by a petiole (Fig. 2B, C, H). In lower combs such a state still partly retained, but in upper combs primordia expanding concentrically and fusing with each other to form a single large comb (Fig. 2C, D, F) although inter-comb boundaries often traceable as slits or empty spaces. 5—Connections between upper and lower combs reinforced by additional petioles (Fig. 2C, H). 6—In spite of such concentric expansion, the final comb shape rather ellipsoid, or irregular (Figs. 1A, 2B, D, G), when influenced by spatial limitation. 7—In mature nests, outer contours of combs often beautifully sinuous (Fig. 2D, F) probably by adjoining development between adjacent primordia and suggesting a mean of expanding support for the wasps involved in nest's defense. 8—Well developed combs very large, 1 m or more in longer axis (Fig. 2C, D). 9—Interspace between combs

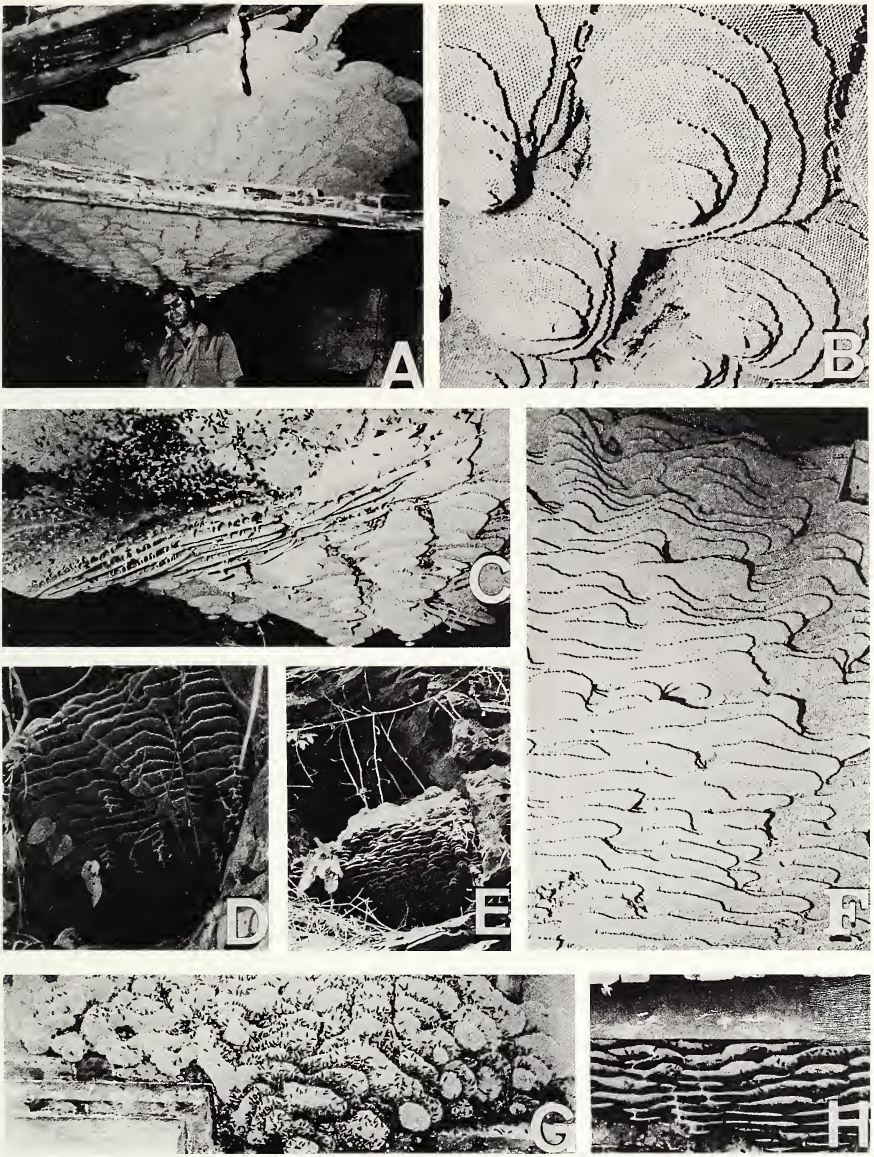

Fig. 2. *Agelaia vicina,* details of nests and nest structure: Nest 3 (A—gross nest shape and size, B—discoidal primordia, C—horizontal combs partially removed to show the brood area inside); Nest 7 (D) and Nest 8 (E) half-exposed in cliff walls; Nest 4 (F—sinuous external limits of combs) and Nest 10 half-exposed at the eaves of a power plant. (G—seen from below, H—seen laterally to show the horizontal combs, pillars and discoidal primordia.)

1.4–2.5 cm. 10—Petioles expanding conically at both ends attached to combs, but cylindrical medially, mostly 2 mm diameter but sometimes 5 mm. 11—Completed cells 6 mm with longer and shorter diameters 2.68 and 2.75 mm, respectively (N = 10 for each measurement). 12—Mean cell number per sq dm 1,127. 13—Meconia and other waste materials sometimes absent in reused young cells suggesting removal through the cell mouth by the adults, but clearly present in reused older cells. 14—Brood concentrated at the nest's core only. 15—Peripheral cells always empty and incomplete probably playing the role of a modified envelope structure, and similar to the envelope-like structure composed of rapidly growing sterile combs found in *A. areata* (Wenzel, 1991).

B. Nests examined

All observed in southern Brazil: Nest 5, in the State of Minas Gerais, the others in the São Paulo State.

Nest 1 (Fig. 1A, B, C) in the collection of Museu do Café, Ribeirão Preto. Illustrated by Costa-Lima (1960:238). Provenance and collection data, unknown. Nesting site unusual, completely unsheltered, built around a coffee tree possibly covered with foliage in the active state 1.65 m high, the largest of 84 combs elliptical, 0.96 × 0.80 m. The whole nest spindle-form, caused by the peculiar nesting site without outward limitation, with middle combs larger than upper and lower ones. Central parts of the combs very irregular with many empty spaces mainly around the trunk and branches (Fig. 1B, C). Assuming each comb to be an ellipse, total comb area 33.58 sq m. Multiplying this with the number of cells per sq dm, total cells estimated at 3,784,466. Regarding parsimoniously each comb as presenting 25% empty spaces (actually certainly less), estimated cell number 2,838,350.

Nest 2. The best studied among the larger nests (Fig. 2A, B, C). Hanging from the ceiling of an abandoned rural house in Fazenda São Gregório, Nuporanga. Examined on Feb. 3, 1976, the surface below was covered with dead wasps from insecticide sprayed three days before. Seen vertically, the whole mass formed an inverted pyramid. From the lowermost incipient cell groups consisting of 31 discoidal areas (Fig. 2A, B, C), 42 comb layers were counted. The gross measures were 2.2 × 2.4 m and 1.1 m (h). Each comb was separated one by one and lain sted side by side. The total comb area was 53.31 sq m and the total number of cells was estimated at 6,008,037, of which 1,983,520 (17.60 sq m) contained the brood (excluding eggs and tiny larvae). Collected dead wasps were sorted to workers (482,668), queens (770) and males (716) by comparing the total weight of adult wasps collected to the weight of a numerically known sample. (For caste differences, von Ihering, 1903; and Sakagami et al., in prep.) However, these values represent only a fraction of adult wasps, all collected in the kitchen, where the nest had been built. Many more remained in the other three rooms, of which the abundant crevices in the damaged wooden floor were full of dead wasps difficult to extract. A search outside revealed many corpses within a radius of 12 m. Moreover, we were told that the fear of the wasps resulted in spraying very inefficiently done. Spray was applied quickly before the dawn through an half-opened window and so the poison reached only one side of the nest. Actually thousands of live callows were present in the core part of the nest (Fig. 2C). The next day a cloud of flying wasps was seen around

Table 1. *Agelaia vicina*: composition of two small but closely analyzed nests.

	Nest 6		Nest 10	
	Frequency	%	Frequency	%
Unused often incomplete fresh cells	470,181	36.44	557,769	74.15
Empty previously used fresh cells	449,379	34.99		
Eggs in fresh cells	2,822	0.21	47,203	6,27
Eggs in reused cells	94,198	7.29		
Small larvae	24,608	1.90	57,783	7.68
Medium larvae	22,050	1.70		
Large larvae	63,328	4.90	89,387	11.88
Cocoons with immatures	164,394	12.77		
Total	1,386,210	99.96	752,139	99.98
Nest's total area (sq m)	12.30	—	6.67	—
Adult wasp:				
workers	157,205	97.05	208,748	97.98
queens	4,717	2.91	672	0.31
males	58	0.03	3610	1.69
total	161,980	99.99	213,030	99.98

the house, evidencing the survival of many adults and suggesting an absconding event. The accurate estimation of the colony population was impossible because of the inevitable partial sampling and plausible migration, but it is sure enough that the number of actually collected wasps represents, even conservatively, about a half of the total adult population, which thus attained over one million wasps. The low queen number found (cf. Nest 10 and Table 1) favors the absconding hypothesis. The queens of the congeneric *A. pallipes* normally gather side by side mainly in the brood area (D. Simões, pers. comm.) which, as in the present case, involves the core of the nest. So, it is likely that many queens protected by combs and worker masses could survive and participate in the subsequent absconding.

Nest 3. Although half-broken when examined, the largest among all closely studied nests (cf. Nest 8, also). Hanging from the ceiling of a brick rural cottage in Santa Rita do Passa Quatro. Abandoned due to poisoning about three months before examination on April 2, 1975. Central part largely damaged but, judging from contour of the remaining parts, about 25% larger than Nest 2, hence approximately with 7,510,046 cells.

Nest 4 (Fig. 2F). An abandoned nest found in a hut about 2 km away from Nest 2 and examined on the same day. The hut, made of bundled grass stems, was a temporary shelter of the kind used by local people, 2.5 m × 2.0 m × 1.8 m (h). Smaller than Nests 2 and 3, 2.23 m × 1.33 m × 0.97 m (h), with the basal surface consisting of 28 discoidal primordia and 48 horizontal comb layers. Its size was estimated at 5,500,000 cells.

Nest 5. Built in a recreation house of sporadic use, in Sacramento. Examined in late March, 1976, after insecticide treatment. Clearly smaller than the previous nests, 1.05 m × 0.67 m × 0.60 m (h). Although not closely studied, the nest is interesting for evidencing the end of gyne production. Many adult workers were found dead among combs, but all recognizable pupae in cells were gynes, whose cocoons differ

from those of workers, being about 1.5 mm high, milky and tough. The rather small nest size indicates colony maturity (reproductive phase), reached much earlier than the realization of the maximum colony size. A similar conclusion can be drawn from the similar sized colony examined by von Ihering (1903) as he found among the true queens many uninseminated gynes.

Nest 6. Collected in a farm corn-mill in Rifaina on May 7, 1976, with ether treatment, for the colony was fully active. A small nest, but exact colony and nest sizes could be determined. The nest had occupied a wooden-box (65 cm × 53 cm × 70 cm, h). Wasps entered the combs through several crevices in a lateral part of the box. The box was completely sealed above with the carton-made dorsal part of the top comb which was made thick by the addition of much more wood pulp than usual. On this account the former cells below disappeared almost completely as substituted by many thick pillars which turned this outer envelope spongy-like and about 1 cm thick. Most combs were broken at removal but some ones taken intact exhibited a sharp alternation of different brood stages, suggesting an emergence-oviposition cycle. Total comb area 12.30 sq m, with 1,386,210 cells of the contents given in Table 1. All adults were fixed in Dietrich fluid, then kept in 70% alcohol. Total colony size (157,205 workers, 4,717 queens and 58 males) was estimated using the same method as in nest 2. Nest 6 was also small but probably in a more advanced stage of the reproduction cycle than Nest 5, exhibiting the end of the queen production phase followed by the beginning of the next worker production. The shift was less neat than in Nest 5, but all examined gyne pupae were of more advanced stages than worker ones. The high queen number is surely the outcome of the reproduction phase in which the nest surely was as demonstrated by the presence of very old, callow and young queens living together.

Nests 7 (Pedregulho, Aug, 10, 1976; Fig. 2D), 8 (ditto, Sept. 16, 1976; Fig. 2E), 9 (Rifaina, Oct. 10, 1976). All found in high (more than 30 m) cliff walls being active and impossible to collect. General features as in other nests, but not hanging from a support. Instead, lateral parts of the combs were attached to the lateral wall of the cliff cavity. Combs are larger at the middle, gradually smaller in upper and lower parts, resulting in a rhombic figure seen laterally. Nest 8 is probably the largest we have seen. For the discoidal primordia seen above and below (Fig. 2E) it is clear that a nest can sometimes concomitantly grow upwards and downwards. These peculiar architectural aspects will be discussed elsewhere.

Nest 10 (Fazenda Santa Carlota, Cajuru, May 20, 1993; Fig. 2G, H). Smaller than nest 6 and equally active. Half exposed in the eaves of a power plant about 6m high. Nest composition could be accuratedly determined (Table 1) because it was ether sprayed very early in the morning. Concerning colony cycle it was clearly at an earlier stage than nest 6. Males were abundantly present, but dissected queens (575 out of 672) invariably showed equivalent ovarian conditions, suggesting quite uniform relative age distribution. It seems likely that such queens represent the founder cohort taking part in colony settlement after swarming.

DISCUSSION

Including the three nests examined by von Ihering (1903), one in a hollow trunk and two in man-made constructs, records of 13 *A. vicina* nests are now available.

Nests built in shelters prevail (8 cases) but half-exposed (4 cases) and a completely exposed nest (Nest 1) suggest plastic and synanthropic (8 cases) nest site preference.

The most outstanding trait of *A. vicina* is certainly the production of gigantic colonies. The reliable values are scarce but in Nest 6 and 10, which are rather small, colony size was estimated at 161,908 and 213,030, respectively. In addition, 482,668 wasps were actually collected in Nest 2 as a fraction of certainly over 1 million wasps.

The large colony size of *A. vicina* may be compared with some other social wasps and bees. In bees the colony of the European honey-bee is often cited as populous but rarely attaining 35,000 individuals (Harbo, 1986). In stingless bees, some species of the subgenus *Trigona* construct large colonies and, probably, the largest is *T. amazonensis.* A colony examined in Curicurieri, Alto Rio Negro, AM. was 2.6 m high × 0.6 m wide, with 40 combs and probably 150,000–200,000 bees (Camargo, J.M.F; pers. comm.).

Some populous colonies in social wasps are: *Brachygastra mellifica* 15,000 (Schwarz, 1929); *Protopolybia acutiscutis* (= *P. pumila* auct.) 21,600 (Richards and Richards, 1951); *Agelaia areata* 21,800 (Jeanne, 1975); *Ropalidia montana* 61,000 (Jeanne and Hunt, 1992). The only case comparable to *A. vicina* is *Vespula germanica,* introduced to New Zealand and Tasmania. In Europe this species is annual, with the maximum colony size (number of adults emerged) not much exceeding 10,000 (Spradbery, 1973). In the introduced areas some colonies overwinter and continue to the next autumn, attaining colossal nest and colony sizes (Thomas, 1960; Spradbery, 1973). The largest aerial nest reached 4.6 m long and 2.4 m wide with about 180 combs, probably containing 3–4 million cells and over 300,000 workers. This example is noteworthy and it demonstrates the potential of the species under artificial induced situations, not the normal development exhibited in the autochthonous condition. A similar situation occurs in Brazil. The hybrids of the introduced African bee *Apis mellifera scutellata* can form huge colonies probably through the joining of several swarms in the course of the migration (Kerr, W.E.; pers. comm.). Unfortunately, such an interesting event remains unexplored.

It must be mentioned that gigantic colonies of wasps and bees are far exceeded by some ants. Only two extreme cases are cited: 1—a migratory colony of the African driver ant *Anomma wilverthi* contained, despite monogyny, 15–22 million workers (Raignier and van Boven, 1955). 2—a polydomous supercolony of *Formica* (*Formica*) *yessensis* which had been extended for 20 km along Ishikari Shore, Japan (now dismembered and nearly exterminated), consisted of 72,000 nests, or 35 million ants (Itô, 1971, 1973).

Besides the colossal colony size, von Ihering (1903) discovered another peculiarity of *A. vicina,* distinct morphological differences between queens and workers. This aspect will be detailed in another paper. Here a few words are given on some bionomic aspects of *A. vicina,* for which answers would be fascinating though very difficult to obtain: 1—Whether mature colonies issue swarming parties larger than in other epiponine species or more numerous but same sized parties as in other species? 2—How long is the foraging distance of each worker? What animals are the principal prey? How is foraging ability balanced with the prey density? 3—What factors mainly regulate the colony density? 4—What animals are principal enemies

and how these are effectively defended? 5—Why and how does this species realize such large colony size?

ACKNOWLEDGMENTS

The authors acknowledge: the financial support by Fapesp (Fundação de Amparo à Pesquisa do Estado de São Paulo) and Capes (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior); Dr. Antonio Barioni Gusman and Dr. Evandro Camillo (University of São Paulo, Ribeirão Preto) Paulo Testa (Batatais, SP), for information on nests; Dr. Dercio Simões and Dr. Nivar Gobbi (Dept. of Zoology, UNESP, Rio Claro, São Paulo) and Marcio Pereira (University of São Paulo, Ribeirão Preto) for several laboratory aid, Director of the Museu do Café (Ribeirão Preto, SP) who gave permission for photographs (Nest 1). Dr. John W. Wenzel (Ohio State University), Dr. James Carpenter (American Museum of Natural History) and Dr. Junichi Kojima (Ibaraki University) for their reading through the typescript and helpful suggestions.

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Received 25 October 1995; accepted 4 January 1996.